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HENRY H. P. SEVERIN

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ADDITIONAL HOST PLANTS OF CURLY TOP

HENRY H. P. SEVERIN*

INTRODUCTION

In a recent paper,⁽⁹⁾ the host plants of curly top in the families Chenopodiaceae, Leguminosae, and Cucurbitaceae were given. Forty varieties of economic plants were reported to be naturally infected with curly top and 120 varieties were experimentally infected with the disease. Eight different species of weeds were demonstrated to be naturally infected with curly top, and nineteen weeds and shrubs to be experimentally infected with the disease.

During 1925 several varieties of peppers failed owing to curly top in the interior regions of California.⁽⁶⁾ McKay⁽⁵⁾ reported as high as 90 per cent of the peppers affected with curly top at The Dalles, Oregon, during 1926. Crawford⁽³⁾ found a large percentage of Chili peppers affected with curly top in New Mexico during 1927.

According to Crawford† the experimental planting of tobacco (*Nicotiana rustica*) at the State College, New Mexico, was entirely destroyed by curly top. Tobacco was infected with the disease near Albuquerque. E. G. Beinharts also reported that tobacco was infected with curly top in Arizona.

During the 1925 outbreak of the beet leafhopper, horse-radish was demonstrated to be naturally infected with curly top in the Sacramento Valley.⁽⁶⁾ According to McKay,⁽⁵⁾ horse-radish was seriously infected with curly top in Oregon during 1926, and in some fields as high as 95 per cent of the crop was diseased.

* Assistant Entomologist in the Experiment Station.

† Letter to author dated October 20, 1927.

In this paper, additional host plants of curly top in the families Solanaceae, Cruciferae, Umbelliferae, Malvaceae, Linaceae, Boraginaceae, and Valerianaceae are listed. Field investigations to determine the economic plants naturally infected with curly top were started during the 1925 outbreak of the beet leafhopper and continued over a period of four seasons. Investigations to ascertain the weeds which were naturally and experimentally infected with this disease was begun in 1918 and has been continued for a period of eleven years.

SOLANACEAE, NIGHTSHADE FAMILY

Potato (Solanum tuberosum).—Volunteer potato plants growing in a vegetable garden on the Spreckels ranch near King City were proved to be naturally infected with curly top during the 1925 outbreak of the beet leafhopper. Non-infective leafhoppers after feeding on 18 potato plants removed from the field transmitted curly top to beets from 14 of the plants. A diseased potato plant growing on the University Farm at Davis and determined as curly dwarf by J. T. Rosa was also demonstrated to be naturally infected with curly top.

A shipment of potato tubers grown on the University Farm was received on November 11, 1925, from J. T. Rosa, who wrote: "I am sending tubers of Irish potatoes that were exposed to leafhoppers and which became yellow and sickly, in my fall crop here. Will you plant them to test tuber transmission of curly top in potato?" The tubers were kept over winter, but curly top was not transmitted to beets during the following spring from any of the 12 potato plants grown. No tests had been made, however, during the autumn to determine whether the potato plants were naturally infected with the disease. Future experiments will show whether tuber transmission of curly top occurs in potatoes. It is known that the disease is carried over in stechlings and mother beets and seriously reduces seed production.

Twelve small potato plants growing on the University Farm at Davis were infected with curly top on May 17, using two leaf-cages each containing 10 nymphs to a plant. Each plant was again infected with the disease on May 30 and June 6, using a total of 60 nymphs. Non-infective beet leafhoppers after feeding on several tips removed from each plant were transferred to 12 sugar beets but only 3 developed curly top.

The following varieties of potatoes were experimentally infected with curly top: American Wonder, British Queen, Idaho Gems, Idaho Rurals, Red Prizetaker or Improved Early Rose, White Rose, White Rose Low-Top, and Wisconsin Pride.

The potato plants naturally infected with curly top were stunted, with yellowish, inward-rolled leaflets. Some of the potatoes infected with curly top on the University Farm showed an inward roll of the leaves, but after the potatoes were irrigated the plants appeared normal. Toward the end of June the leaves on the lower portion of a few of the infected potatoes turned orange yellow in color, but many plants not infected with the disease showed a similar discoloration of the foliage.



Fig. 1. White Rose Potato (*Solanum tuberosum*) experimentally infected with curly top, showing terminal shoots with inward-rolled leaflets and bent petioles.

In the greenhouse the eight varieties of potatoes experimentally infected with curly top also showed an inward roll of the leaflets and often a bending of the petioles (fig. 1). Potatoes in an advanced stage of the disease frequently developed dwarfed shoots in the axil of the leaves (fig. 2), near the tip of the plants. Later the plants turned yellow and died.

Tomato (*Lycopersicon esculentum*).—The proof that the beet leafhopper transmits curly top to tomatoes has appeared in a previous paper.⁽⁷⁾

Peppers (*Capsicum frutescens*).—During 1925, investigation of a field of Pimiento peppers grown near Freeport in the Sacramento Valley showed that 78 per cent of the crop was stunted, with thick, leathery inward-curved leaves. Curly-top beets had been plowed under

in the vicinity of this pepper field, forcing the beet leafhoppers to seek other food plants. Peppers similarly affected were also found in a field a few miles west of the city of Sacramento. Four varieties of peppers grown on the Spreckels ranch near King City were dwarfed; many of the plants were only 8 to 12 inches tall and often dry, while

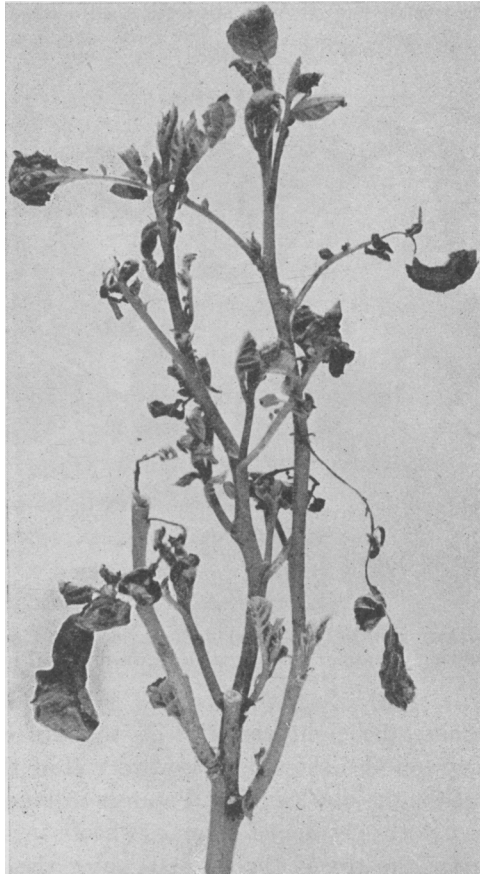


Fig. 2. White Rose Low-Top potato (*Solanum tuberosum*) in an advanced stage of curly top, showing numerous dwarfed shoots and drying of some of the leaves.

others were about one-half of their normal size. Shipments of stunted Pimiento peppers grown by the California Packing Corporation at Armona, Kings County, in the San Joaquin Valley were sent to the University of California. Fruit was usually absent on the smallest plants but on the somewhat larger ones, small malformed fruit was

present (figs. 3, 4). Non-infective beet leafhoppers, however, did not transmit curly top from all of the dwarfed varieties of pepper plants removed from the field to sugar beets.



Fig. 3. Paprika pepper (*Capsicum frutescens*): stunted plant naturally infected with curly top, showing curled, dwarfed leaves on the terminal shoots, and malformed fruit.

The following varieties of pepper were proved to be naturally infected with curly top: Anaheim Chili, Paprika, Pimiento, and Mexican Chili.

When the four varieties of pepper naturally infected with curly top in the Salinas Valley were shaken, an occasional adult but rarely a nymph hopped from the plants.

Non-infective beet leafhoppers when allowed to feed on the fruit of naturally infected Anaheim Chili and Pimiento peppers with the stems removed transmitted curly top to sugar beets.

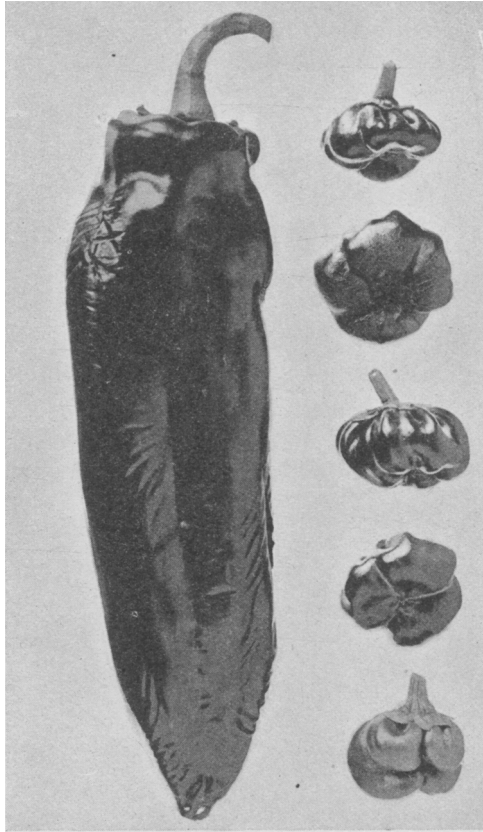


Fig. 4. Paprika pepper (*Capsicum frutescens*): fruit from healthy plant, and five dwarfed, malformed fruits from plant naturally infected with curly top.

The following varieties of peppers were experimentally infected with curly top: Anaheim Chili, California Wonder, Chinese Giant, Large Bell or Bull Nose, Long Red Cayenne, Mexican Chili, Pimiento, Red Chili, Royal King, Ruby King, Sweet Mountain, Sweet Upright, and Tobasco. The following varieties of pepper-tomato were also experimentally infected with the disease: Ignacio, Novata, Petaluma, San Geronimo, Sonoma, Topepo, and Tulare.

As a general rule, an inward curl of the youngest leaves and an outward cupping of the somewhat older leaves occurred in the first thirteen varieties of peppers listed. The veinlets became transparent on the youngest leaves. Transparent venation, however, has never been observed in naturally infected peppers, but no observations have been made on young plants. Minute swellings developed on the network of cleared veinlets resembling somewhat the warty protuberances on the leaves of sugar beets in an advanced stage of curly top.

In the seven varieties of infected pepper-tomatoes, some of the leaflets showed an inward curl, and sometimes the petioles of two adjacent leaflets were bent so that the upper surfaces of the leaflets were in contact or the youngest leaves were very much twisted (pl. 1). White swellings sometimes appeared on the lateral veins of the youngest leaves. A yellowing developed between the lateral veins, while the veins remained green. In the later stages of the disease the plants were decidedly yellow.

The longevity of the last living male and female beet leafhopper on the different varieties of peppers was as follows:

Variety of pepper	Longevity of males days	Longevity of females days
Anaheim Chili.....	4- 5	7
California Wonder.....	1- 6	2- 9
Chinese Giant.....	4	8
Large Bell or Bull Nose.....	7	10
Long Red Cayenne.....	4- 7	10
Mexican Chili.....	7	8
Pimiento.....	3- 5	5-12
Red Chili.....	2- 4	10
Royal King.....	2- 3	3- 6
Ruby King.....	3- 6	5-12
Sweet Mountain.....	4- 6	10
Sweet Upright.....	4	5
Tobasco.....	2- 8	12-14
Ignacio pepper-tomato.....	3- 4	11
Novata pepper-tomato.....	3- 5	11
Petaluma pepper-tomato.....	3- 5	12
San Geronimo pepper-tomato.....	6-10	10
Sonoma pepper-tomato.....	3- 4	8
Topepo pepper-tomato.....	2- 4	5- 6
Tulare pepper-tomato.....	3- 4	12

It is evident that the males lived from 1 to 10 days and the females from 2 to 14 days on the different varieties of peppers.

Tobacco (Nicotiana tabacum).—The following varieties of tobacco were experimentally infected with curly top: Big Havana, Connecticut Broad Leaf, Connecticut Seed Leaf, Sumatra, Turkish, and White Burley.

The first symptom to develop in the six varieties of tobacco experimentally infected with curly top was a clearing of the veinlets. A marked stunting of the infected plants occurred with a shortening of the internodes. The youngest leaves were dwarfed and outwardly cupped (fig. 5).

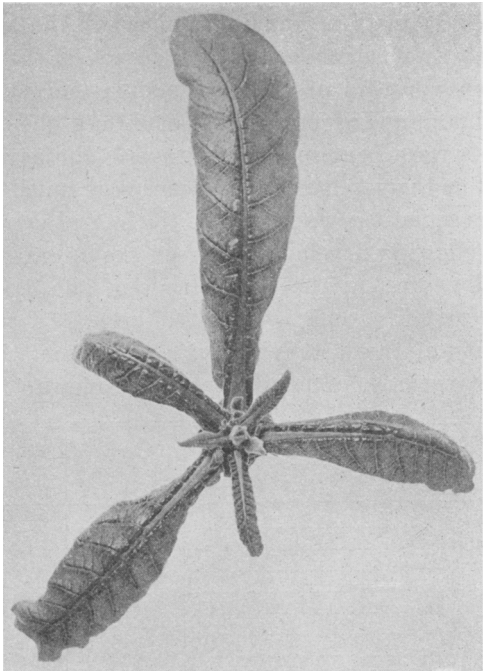


Fig. 5. White Burley tobacco (*Nicotiana tabacum*) experimentally infected with curly top, showing dwarfed youngest leaves, outward-cupped older leaves, and shortening of the internodes.

The adult life of the last living male and female beet leafhoppers on the different varieties of tobacco was as follows:

Variety of tobacco	Longevity of males days	Longevity of females days
Big Havana.....	4	5-14
Connecticut Broad Leaf.....	3- 4	6-12
Connecticut Seed Leaf.....	4- 8	4- 6
Sumatra.....	3	6-11
Turkish.....	4-10	3-10
White Burley.....	3- 5	13

The results show that the males lived from 3 to 10 days and the females from 3 to 14 days on a tobacco diet.

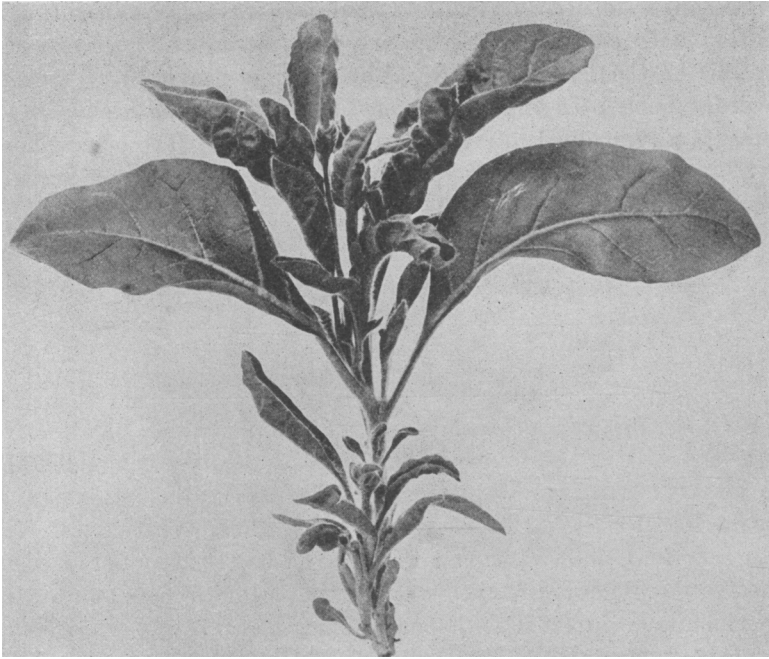


Fig. 6. Peasant's tobacco (*Nicotiana rustica*) experimentally infected with curly top, showing secondary shoots growing from the axil of the leaves, with dwarfed, inward-curved leaves.

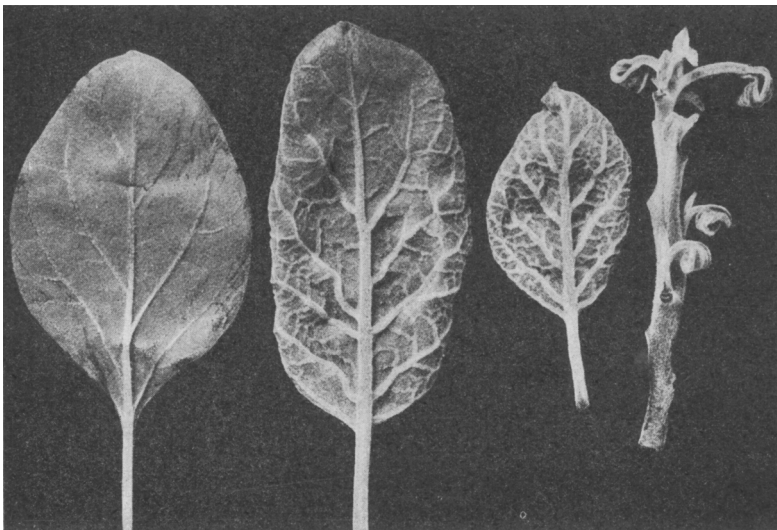


Fig. 7. Peasant's tobacco (*Nicotiana rustica*): left, venation of healthy leaf; transparent venation on next two leaves from plant infected with curly top; right stem showing dwarfed youngest leaves with terminal ends rolled toward petioles.

Peasant's tobacco (*Nicotiana rustica*) was also experimentally infected with curly top. Secondary shoots frequently developed in the axil of the leaves (fig. 6). The younger leaves were dwarfed, inwardly curled (fig. 6) and sometimes the terminal ends of the youngest leaves rolled toward the petioles (fig. 7). The leaves showed the cleared veinlets. The average longevity of the adults on Peasant's tobacco varied according to the age of the plants, as follows:

Height of Peasant's tobacco	Longevity of males days	Longevity of females days
4-8 inches.....	10	15
12-36 inches.....	59	63

Life History of Beet Leafhopper.—Nymphs which hatched from eggs deposited in the following varieties of potatoes completed their life history: American Wonder, British Queen, Idaho Gems, Idaho Rurals, Red Prizetaker or Improved Early Rose, White Rose, White Rose Low-Top, and Wisconsin Pride. The beet leafhopper, however, failed to complete its life cycle on all varieties of peppers and tobaccos experimentally infected with curly top.

Weeds.—During the 1925 outbreak of the beet leafhopper, stunted plants of deadly nightshade (*Solanum nigrum douglassi*) with dwarfed leaves at the terminal end of the shoots, inward-curved older leaves, and secondary shoots growing from the axil of the leaves (fig. 8) were frequently observed in the beet fields of the Salinas Valley and in the San Joaquin Valley near Manteca. Three plants showing these symptoms were removed from the beet fields near Greenfield in the Salinas Valley and 12 were taken from the beet fields near Manteca. Non-infective beet leafhoppers after feeding on these 15 weeds transmitted curly top to 11 of 15 sugar beets. During the years between the 1919 and 1925 outbreaks of the beet leafhopper, this weed was rarely found to be naturally infected with the disease.

Deadly nightshade plants grown from seeds were repeatedly inoculated by different lots of from 5 to 50 infective male beet leafhoppers. The males lived from 3 to 11 days on this weed, and as soon as one batch of infective leafhoppers died another lot was placed on each plant. Non-infective hoppers after feeding on 10 plants inoculated with the disease by successive lots of 5 or 10 adults, transmitted curly top to 3 beets, while 7 beets remained healthy. One of 7 plants inoculated by successive lots of from 25 or 50 infective males, was shown to be experimentally infected with the disease. The experimentally infected plants showed a marked inward roll of the terminal leaves

(fig. 9). In all probability, mass infection is not a factor in curly-top infection of this weed. Whenever a severe epidemic of curly top occurs, the disease is apparently more virulent and weeds which are highly resistant seem to become more susceptible to the disease.



Fig. 8. Deadly nightshade (*Solanum nigrum douglassi*) naturally infected with curly top, showing secondary shoots growing from the axil of the leaves, with dwarfed leaves at the terminal end of the shoots.

Ground cherry (*Physalis wrightii*) growing in a beet field near Manteca was demonstrated to be naturally infected with curly top during the 1925 outbreak of the beet leafhopper.

Stramonium (*Datura stramonium*) was experimentally infected with curly top. The youngest leaves were dwarfed (pl. 2, fig. 2) and showed the transparent veinlets (pl. 2, fig. 2, insert).

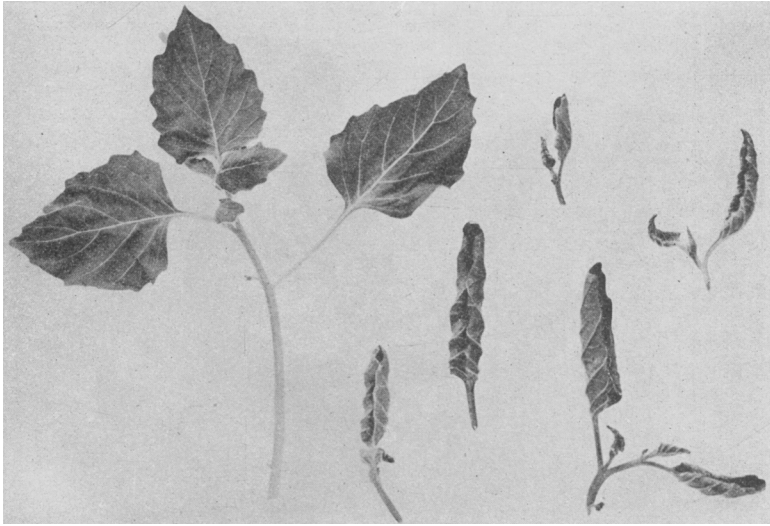


Fig. 9. Deadly nightshade (*Solanum nigrum douglassi*): left, shoot from check or control plant on which non-infective male beet leafhoppers had fed; right, five shoots and leaves from experimentally infected plants, showing inward-rolled youngest leaves.

CRUCIFERAE, MUSTARD FAMILY

During the 1925 outbreak of the beet leafhopper, numerous tests were made with a large number of Cruciferae to determine the natural host range of curly top in this family. Economic crucifers naturally infected with curly top are difficult to recognize in the field as most species show no reliable foliage symptoms of the disease. Plants on which the beet leafhoppers were collected in the field were removed with the root system, transplanted in flower pots and tested in the greenhouse.

Different varieties of crucifers grown from seeds were inoculated with curly top by infective beet leafhoppers, but the transmission of the disease by non-infective hoppers after feeding on the inoculated plants to sugar beets was not often accomplished. During the spring and summer of 1926, Henderson⁽⁴⁾ inoculated a large number of crucifers, usually using 6 plants of each variety. In view of the fact that an occasional plant of some varieties was experimentally infected

with the disease, all varieties which were shown to be susceptible to curly top were again tested during 1927. During 1928, J. H. Freitag again repeated the work with all varieties which had previously been experimentally infected with the disease. During the four years a total of 18 plants of all susceptible varieties were inoculated by infective beet leafhoppers. The plants were usually inoculated after acquiring from 2 to 6 leaves.

Horse-Radish (Armoracia rusticana).—Horse-radish was demonstrated to be naturally infected with curly top. The beet leafhoppers were found abundant on June 17, 1925, in a quarter acre of horse-radish near Walnut Grove in the Sacramento Valley. The horse-radish was adjacent to a badly diseased beet field which had become so weedy that the beet foliage and weeds were cut by mowing. Nymphs in all stages of development were present on the foliage of horse-radish, and when the leaves were shaken the ground became covered with a multitude of hoppers. The horse-radish field was visited once a month from June to September, and an enormous increase of leafhoppers occurred, corresponding in numbers to those found in beet fields. In a vegetable garden on the Spreckels ranch near King City in the Salinas Valley the adults were scarce on a few horse-radish plants and no nymphs were observed.

Horse-radish plants with an inward curl of the leaves (fig. 10) were common. The sap exuded from the petioles of some of the leaves in a manner similar to curly-top beets. During the summer the foliage of many plants turned yellow. Horse-radish plants which had become dry were found here and there in this field during June, but in September many plants were dead.

The roots of horse-radish plants infected with curly top early in the season were dwarfed and brittle. A cross section of a diseased root shows darkened rings and bundles in the interior (pl. 3, fig. 2) while a longitudinal section shows the dark discolorations extending lengthwise through the root (pl. 3, figs. 1, 2).

Cuttings from diseased roots sometimes failed to sprout, or a large number of spindling shoots (pl. 3, fig. 1) developed and died before reaching or growing through the surface of the soil. If the shoots continued to grow the plant was stunted and the root did not increase in size.

Curly top was rarely transmitted from diseased horse-radish grown in this field to sugar beets. Twenty-two diseased horse-radish plants were removed from the soil with the root system and transplanted to flower-pots in the greenhouse. Non-infective beet leafhoppers after

feeding on the 22 plants transmitted curly top to 3 of 22 sugar beets. During September the youngest leaves and a few outer leaves with sap often exuding from the petioles were removed from a large number of plants. Thirty-six lots of non-infective males confined in cages were fed on the leaves for a period varying from 6 to 11 days, and were then transferred to 36 beet seedlings, but not a single case of curly top developed.

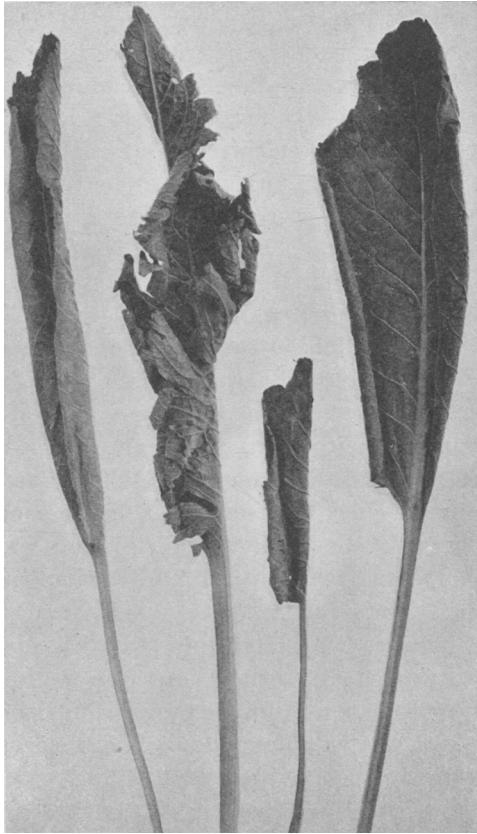


Fig. 10. Horse-radish (*Amoracia rusticana*), showing four inward-rolled leaves from a plant naturally infected with curly top.

It was decided to inoculate, with infective beet leafhoppers, some of the horse-radish plants grown in the field and others propagated from cuttings. Curly top was transmitted by non-infective males feeding on the inoculated plants to sugar beets from 22 of 29 horse-radish plants.

An experiment was now conducted to determine whether beet leafhoppers would continue to transmit curly top from the infected horse-radish plants during a period of three months. Eight lots of 25 non-infective males were fed on 8 infected horse-radish plants during each month and then each lot was equally distributed on 2 healthy beet seedlings. The results obtained are indicated in table 1.

TABLE 1

TRANSMISSION OF CURLY TOP FROM INFECTED HORSE-RADISH TO SUGAR BEETS
DURING A PERIOD OF THREE MONTHS

Horse-radish plant No.	Date of inoculation with infective males	Dates non-infective males fed on inoculated horse-radish plants					
		June 10-15		July 18-23		August 19-23	
		Beets infected	Beets healthy	Beets infected	Beets healthy	Beets infected	Beets healthy
1	May 21-June 10	1	1	2	0	0	2
2	May 21-June 10	1	1	0	2	1	1
3	May 21-June 10	1	1	2	0	0	2
4	May 21-June 10	2	0	2	0	1	1
5	May 11-June 10	2	0	1	1	0	2
6	May 10-June 10	2	0	0	2	0	2
7	May 10-June 10	1	1	0	2	1	1
8	May 21-June 10	2	0	0	2	0	2
Total.....		12	4	7	9	3	13
Number of horse-radish plants from which disease was transmitted.....		8	4	3

Experiments were conducted to determine whether the virus becomes inactivated in horse-radish during the winter. Two of the 3 plants from which curly top was transmitted during a period of three months lived through the winter. During the following spring, non-infective beet leafhoppers after feeding on these 2 horse-radish plants failed to transmit curly top to beets.

Two shipments of naturally infected and apparently healthy roots were received from F. M. McKay during 1927. Cuttings were grown from 47 roots, some of which showed the dark discoloration, while others were white. Non-infective beet leafhoppers after feeding on the leaves of horse-radish were transferred to beets, but not a single case of curly top developed.

Another test was made to determine whether horse-radish plants in which the virus was inactivated during the winter could be reinfected with curly top. Eight plants with darkened areas in the roots were selected from the 47, and inoculated with curly top. Ten infec-

tive males were fed on each plant for a period of 25 days. Ten non-infective males were then fed from 3 to 6 days on each infected plant during each month for a period of four months. The monthly transmission of curly top to beets from such horse-radish plants as survived is shown as follows:

Month	Number of horse-radish plants alive	Number of beets that developed curly top	Number of beets healthy
First.....	8	8	0
Second.....	7	7	0
Third.....	6	5	1
Fourth.....	4	4	0

It appears that the resistant factors associated with the inactivation of the virus during the first year are greatly reduced or absent when horse-radish is reinfected during the second year.

Observations and experiments conducted in the field and greenhouse by McKay indicate that horse-radish from late-infected plants may be white, but when white cuttings were planted, some of these were badly discolored when dug and resulted in a diseased growth in a high percentage of cases. It is evident that after a serious outbreak of curly top in horse-radish fields, cuttings should be made from healthy roots obtained from the Middle West or East, where curly top does not occur.

Radish (Raphanus sativus).—A variety of radish, probably Red Globe, growing in a vegetable garden of the Spreckels ranch near Greenfield in the Salinas Valley, was naturally infected with curly top. The disease, however, was transmitted to sugar beets from only 2 of 15 plants.

Long Black Spanish and Long White Japanese radishes were experimentally infected with curly top, but 17 varieties were not infected with the disease.

The naturally infected radishes showed an inward curl of the leaves with outstanding veins (fig. 11). The two varieties of radishes experimentally infected with curly top showed no reliable foliage symptoms under greenhouse conditions, except a stunting of the plants and a yellowing of the leaves in the later stages of the disease. Long Black Spanish showed a slight inward roll of some of the leaflets, but this also occurred in radishes used as a check or control.

Collards (Brassica oleracea acephala).—Georgia Southern or Creole and True Southern collards were experimentally infected with curly top.

One plant of Georgia Southern or Creole collards showed a dwarfing and malformation of the youngest leaves with shortened petioles (fig. 12) but other infected plants developed no such symptoms.



Fig. 11. Radish (*Raphanus sativus*) naturally infected with curly top, showing inward-curved leaves with outstanding veins. The variety was determined by J. T. Rosa as probably Red Globe.

Garden Cabbage (*Brassica oleracea capitata*).—Curly top was transmitted to sugar beets from an unknown variety of cabbage growing in a vegetable garden of the Spreckels Sugar Company near King City in the Salinas Valley during 1925.

The following varieties of cabbage were experimentally infected with curly top: All Head Early, Early Jersey Wakefield, Early Winningstadt, Improved American Savoy, Charleston, Wakefield, Large Flat Dutch, Large Late Drumhead, Mammoth Red Rock, and Surehead.

Among all of the experimentally infected varieties of cabbages listed, infective beet leafhoppers inoculated many plants from which



Fig. 12. Georgia Southern or Creole collards (*Brassica oleracea acephala*) experimentally infected with curly top, showing dwarfed and malformed youngest leaves with shortened petioles.

non-infective males failed to transmit the disease to sugar beets. In some of the experiments different varieties of cabbages were planted on the same date, infected with the same number of hoppers, and exposed to the same temperatures and sunlight; but under these conditions some plants were infected with curly top while others were not.

Naturally infected cabbage showed no reliable foliage symptoms of curly top. Sap sometimes exuded from the petioles and veins of varieties infected in the greenhouse.

Cauliflower, Broccoli (*Brassica oleracea botrytis*).—Early Snowball, Large White Cape, Purple Cape, and St. Valentine were experi-

mentally infected with curly top. Two St. Valentine broccoli showed a whitening of the veinlets on a portion of the younger leaves, but non-infective beet leafhoppers failed to transmit curly top to sugar beets from these plants. The white venation disappeared later.

Turnip (Brassica rapa).—Curly top was transmitted to sugar beets from 7 to 35 stunted Purple Top Globe turnips growing in a vegetable garden of the Spreckels ranch near Greenfield.

The following varieties of turnips were experimentally infected with curly top: Cow Horn or Long White, Early Purple Top, Flat Dutch, and Seven Top.

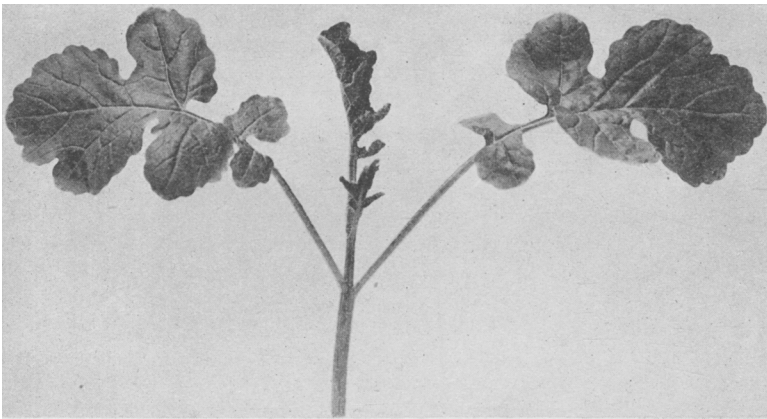


Fig. 13. Terminal shoot of White London mustard (*Brassica alba*) experimentally infected with curly top, showing youngest leaves curled inward along the mid-rib.

Turnips showed no reliable foliage symptoms of curly top. In some varieties a cupping or slight inward rolling of the leaves developed, but this also occurred in the check or control plants. One plant of Cow Horn or Long White turnip showed a shortening of the petioles of the youngest leaves, but other infected plants were apparently normal.

White London Mustard (Brassica alba).—White London mustard was experimentally infected with curly top. The youngest leaves of infected plants were dwarfed and curled inward along the mid-rib (fig. 13).

Chinese, Celery Cabbage, or Wong Bok (Brassica pekinensis).—Four plants removed from the field and 8 plants grown from seeds were non-susceptible to curly top.

Chinese Cabbage, probably Chosen and Pe-tsai (Brassica pekinensis).—Two varieties of Chinese cabbage appeared to be naturally infected with curly top; the youngest leaves were dwarfed and curled, but non-infective beet leafhoppers failed to transmit the disease to sugar beets.

Cress (Barbarea vulgaris).—Two varieties of cress, Fine Curled and True Water, were experimentally infected with curly top.

The youngest leaves of Fine Curled cress were curled (fig. 14) and showed faint indications of transparent venation. True Water



Fig. 14. Fine Curled cress (*Barbarea vulgaris*): four curled leaves from a plant experimentally infected with curly top; right, leaf from check or control plant on which non-infective male beet leafhoppers fed.

cress showed (pl. 2, fig. 1) a shortening of the petioles at the terminal end of the shoots, an inward roll of the leaflets, and sometimes elevations on the lower surface of the leaves.

Natural Breeding Plants of Beet Leafhopper.—Nymphs which hatched from eggs deposited in the foliage of the following Cruciferae removed from the field acquired the winged stage: horse-radish, unknown variety of cabbage, and Purple Top Globe and Early White Flat Dutch turnips. Nymphs in all stages of development and adults were abundant on horse-radish, and Purple Top Globe and Early White Flat Dutch turnips, but rare on garden cabbage during 1925. Adults were commonly found on radish but no nymphs were observed when the foliage was disturbed with the hand.

Life History of Beet Leafhopper.—The beet leafhopper completed its life history in the greenhouse on the following varieties of Cruciferae:

Horse-radish (*Armoracia rusticana*).

Radish (*Raphanus sativus*): California or Chinese White Winter, China Rose Winter, Crimson Giant, Early Scarlet Globe, Early Scarlet Turnip, French Breakfast, Half Long Deep Scarlet, Icicle or White Icicle, Long Black Spanish, Long Scarlet, Long White Japanese, Round Black Spanish, Siberian, Winter or Chinese White Winter, White Tip Scarlet Turnip, and White Vienna.

Kale, borecole (*Brassica oleracea acephala*): Dwarfed Curled Scotch, Giant Marrow, Jersey or Thousand Headed, and Tall Curled Scotch.

Collards (*Brassica oleracea acephala*): True Southern.

Brussels sprouts (*Brassica oleracea gemmifera*): Cooper's Selected Aigbruth, Danish Giant, Dwarf Perfection, and Morse's Brussels sprouts.

Garden cabbage (*Brassica oleracea capitata*): All Head Early, All Season, Autumn King, Copenhagen Market, Danish Ball Head, Drumhead Savoy, Early Flat Dutch, Early Jersey Wakefield, Early Winningstadt, Improved American Savoy, Late Flat Dutch, Large Early Wakefield, Large Flat Dutch, Large Late Drumhead, Mammoth Red Rock, and Surehead.

Cauliflower, Broccoli (*Brassica oleracea botrytis*): California Wonder, Dry Weather, Early Snowball, Improved Autumn Giant, Large White Cape, Morse's February, Morse's April, Purple Cape, St. Valentine, and Veitch's Autumn Giant.

Kohlrabi (*Brassica oleracea caulorapa*): Early White Vienna and Early Purple Vienna.

Rutabaga (*Brassica napobrassica*): American Purple Top and Purple Top Yellow.

Turnip (*Brassica rapa*): Amber Globe, American Purple Top, Cow Horn or Long White, Early Purple Top, Early Purple Top Milan, Early White Flat Dutch, Orange Jelly or Golden Ball, Purple Top Strapped-leaved, Purple Top White Globe, Seven Top, Snowball, White Egg, and White German.

Chinese mustard (*Brassica juncea*).

Southern Curled mustard (*Brassica juncea crispifolia*).

Chinese, Celery cabbage, or Wong Bok (*Brassica pekinensis*).

Black mustard (*Brassica nigra*).

White London mustard (*Brassica alba*).

Weeds.—Charlock (*Brassica arvensis*) growing in a beet field near Hamilton City in the Sacramento Valley was demonstrated to be naturally infected with curly top during 1918.

Shepherd's purse (*Capsella bursa-pastoris*) growing in a beet field near Greenfield in the Salinas Valley was proved to be naturally infected with curly top during 1925. This weed grown from seed was also experimentally infected with the disease. The infected plants were stunted with twisted seed stalks (fig. 15) usually bearing malformed seeds (fig. 16) near the terminal ends.



Fig. 15. Shepherd's purse (*Capsella bursa-pastoris*) naturally infected with curly top, showing twisted seed stalks.

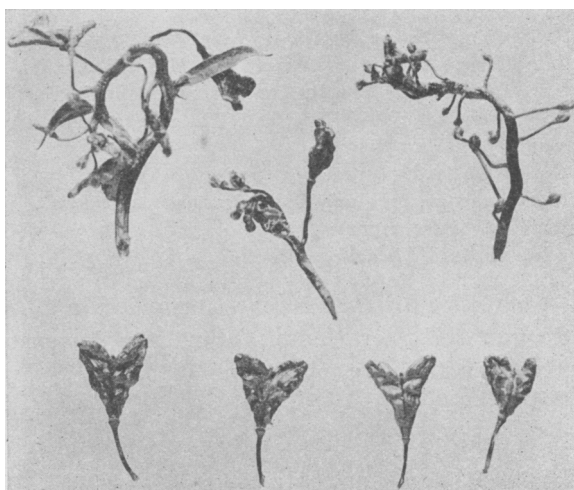


Fig. 16. Shepherd's purse (*Capsella bursa-pastoris*): upper row, terminal ends of twisted seed stalks, showing malformed seeds; lower row, seeds from lower region of seed stalks.

POLYGONACEAE, BUCKWHEAT OR KNOTWEED FAMILY

Common Buckwheat (*Fagopyrum esculentum*).—Common buckwheat was experimentally infected with curly top. The first symptoms to appear were blister-like elevations on the youngest leaves, then the margins of the youngest leaves rolled inward (fig. 17), with the tissue sunken between the lateral veins, and twisted petioles (fig. 17). In the later stages of the disease the leaves were dwarfed and often cupped outward. The plant finally turned yellow and died.



Fig. 17. Common buckwheat (*Fagopyrum esculentum*): left, tip of plant experimentally infected with curly top, showing inward-rolled youngest leaves with twisted petioles and curled older leaves; right, check or control plant on which non-infective beet leafhoppers fed.

Giant Crimson Winter Rhubarb (*Rheum rhaponticum*).—Giant Crimson Winter rhubarb was experimentally infected with curly top, but showed no reliable foliage symptoms. Curly top was transmitted to sugar beets from 7 of 13 plants inoculated by infective beet leafhoppers.

French Large-leaved Sorrel (*Rumex scutatus*).—French Large-leaved sorrel experimentally infected with curly top developed wart-

like protuberances (fig. 18) on the lower surface of the leaves in the later stages of the disease.

Life History of Beet Leafhopper.—Nymphs which hatched from eggs deposited in the following plants of the Polygonaceae completed their life history in the greenhouse: Common buckwheat, French Large-leaved sorrel, Giant Crimson Winter, and Wagner's Giant rhubarb.

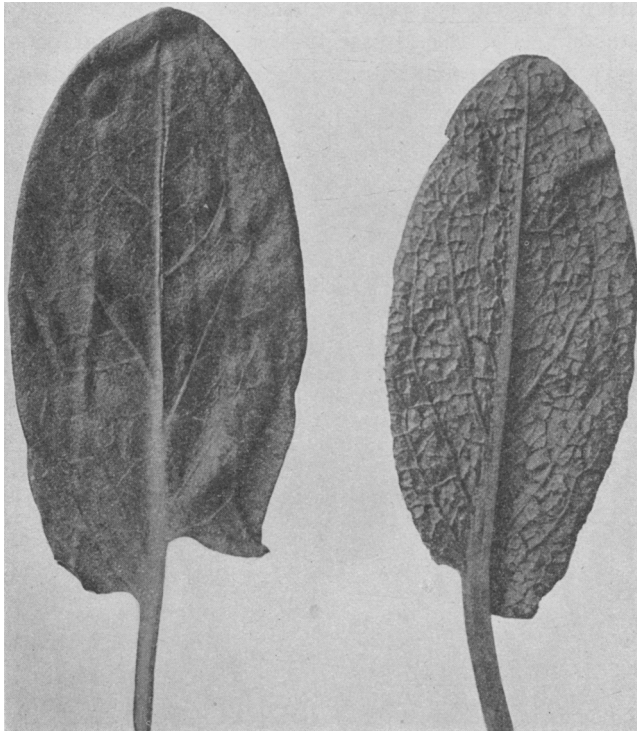


Fig. 18. French Large-leaved sorrel (*Rumex scutatus*): left, leaf from check or control plant on which non-infective beet leafhoppers fed; right, leaf from plant experimentally infected with curly top, showing wart-like protuberances on lower surface.

Weeds.—The following weeds were proved to be naturally infected with curly top: wire grass (*Polygonium ariculare*), swamp smartweed (*P. muhlenbergii*) (fig. 19), water smartweed (*P. amphibian hartwrightii*), common knotweed (*P. lapathifolium*), and a lady's thumb (*P. persicaria*).

Curly dock (*Rumex crispus*) was experimentally infected with curly top and showed wart-like protuberances (fig. 20) on the lower surface of the leaves in the later stages of the disease. The protuberances of the lower surface of the leaves is a reliable and constant symptom of curly top in most economic plants of the Chenopodiaceae, but this symptom failed to develop in cultivated plants and weeds of all families so far investigated except sorrel (*Rumex scutatus*) and curly dock (*R. crispus*) of the family Polygonaceae.



Fig. 19. Swamp smartweeds (*Polygonum muhlenbergii*) naturally infected with curly top, showing inward-rolled leaves.

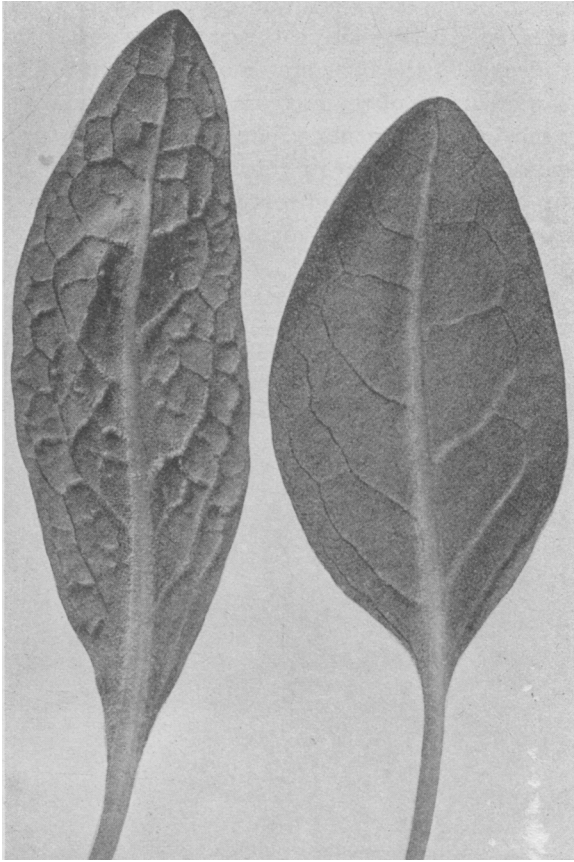


Fig. 20. Curly dock (*Rumex crispus*): left, leaf from a plant experimentally infected with curly top, showing wart-like protuberances on the lower surface; right, leaf from check or control plant on which non-infective beet leafhoppers fed.

UMBELLIFERAE, PARSLEY FAMILY

Coriander (*Coriandrum sativum*).—Coriander experimentally infected with curly top showed a marked curling and twisting of the leaflets (fig. 21).

Dill (*Anethum graveolens*).—Dill was inoculated with curly top by infective beet leafhoppers in the greenhouse and showed a drooping of the leaflets from the curved mid-rib (fig. 22).

Florence Fennel (*Foeniculum dulce*).—Florence fennel experimentally infected with curly top showed a shortening of the petioles

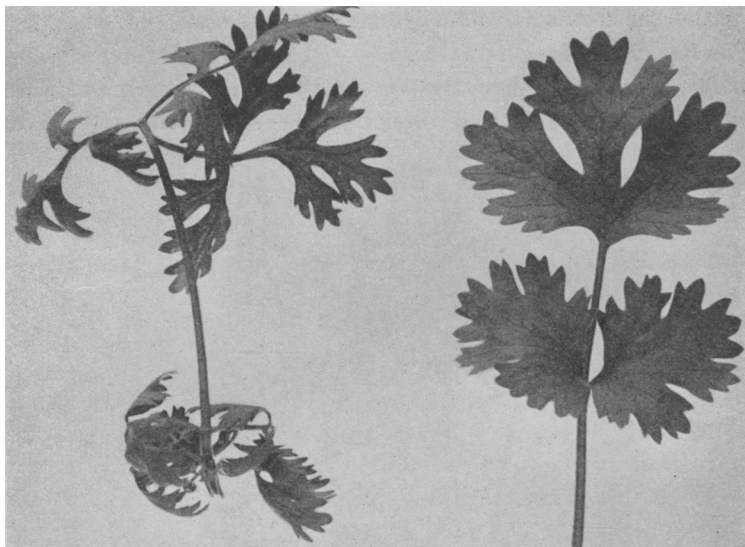


Fig. 21. Coriander (*Coriandrum sativum*): left, leaf from a plant experimentally infected with curly top, showing curled and twisted leaflets; right, leaf from check or control plant.

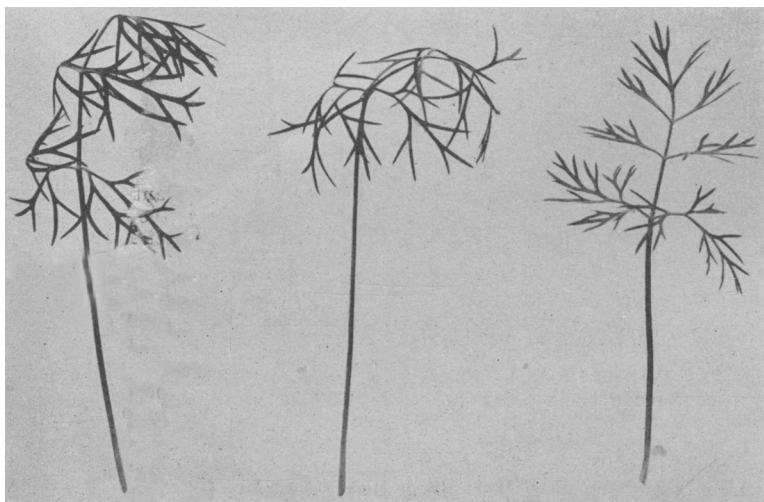


Fig. 22. Dill (*Anethum graveolens*): left, two leaves from a plant experimentally infected with curly top, showing drooping of leaflets from curved mid-rib; right, leaf from check or control plant on which non-infective beet leafhoppers fed.

of the youngest leaves, with curled thread-like leaflets (fig. 23). The petioles of the somewhat older leaves often drooped (fig. 23).

Parsley (Petroselinum hortense).—Plain parsley was proved to be naturally infected with curly top in the Salinas and Santa Clara valleys. During the 1925 outbreak of the beet leafhopper, nymphs



Fig. 23. Florence fennel (*Foeniculum dulce*) experimentally infected with curly top, showing shortened petioles of youngest leaves and curled thread-like leaflets.

and adults were commonly found on parsley growing in the vegetable garden of Spreckels Sugar Company near Chular. Curly top was transmitted to sugar beets from only 2 of 16 plants removed from the field.

The following varieties of parsley were experimentally infected with curly top: Champion Moss-Curled, Fern-Leaf Moss, and Plain.

The disease, however, was rarely transmitted to sugar beets from the different varieties of parsley inoculated by infective beet leafhoppers.

Naturally and experimentally infected parsley showed no visible foliage symptom of the disease.

Celery (*Apium graveolens dulce*).—The results of the investigations on celery infected with curly top in the greenhouse has been published in a previous paper.⁽⁸⁾

Salad Chervil (*Anthriscus cerefolium*).—Salad chervil was infected with curly top in the greenhouse. The symptoms were similar to those of Florence fennel.

Life History of Beet Leafhopper.—Nymphs which hatched from eggs deposited in the following varieties of Umbelliferae acquired the adult stage on these food plants: caraway (*Carum carvi*), coriander, Florence fennel; Champion Moss-Curled, Fern Leaf-Moss, Hamburg or Turnip-Rooted and Plain parsley; Giant Paschal, Golden Self-Blanching and White Plume celery; and salad chervil.

MALVACEAE, MALLOW FAMILY

Okra or Gumbo (*Hibiscus esculentus*).—The following varieties of okra or gumbo were experimentally infected with curly top: Long Green, Perkins Mammoth Long Pod, and White Velvet.

The three infected varieties of okra or gumbo were stunted and showed a slight outward cupping of the youngest leaves. The lower leaves turned yellow and dropped from the plants.

The longevity of the last living male and female beet leafhopper on the three varieties of okra or gumbo was as follows:

Variety of okra or gumbo	Longevity of males days	Longevity of females days
Long Green.....	3-12	3-15
Perkin's Mammoth Long Pod.....	3-13	8-20
White Velvet.....	3-16	14-19

Nymphs which hatched from eggs deposited in okra or gumbo failed to complete their life cycle in the greenhouse.

Acala Cotton (*Gossypium hirsutum*).—A number of letters were received inquiring whether Acala cotton is naturally infected with curly top. An examination of many fields of cotton in the San Joa-

quin Valley failed to show any indication of this disease nor of the beet leafhopper. These observations were made in years between outbreaks of the beet leafhopper; no examinations were made during the 1925 outbreak of the pest.

Acala cotton is non-susceptible to curly top. Twenty plants grown from seeds were repeatedly inoculated by different lots of 10 infective beet leafhoppers. As soon as the 10 hoppers had died on each plant another batch of 10 was put in the cage enclosing each plant. In this experiment 1,000 infective males were used to inoculate the 20 plants.

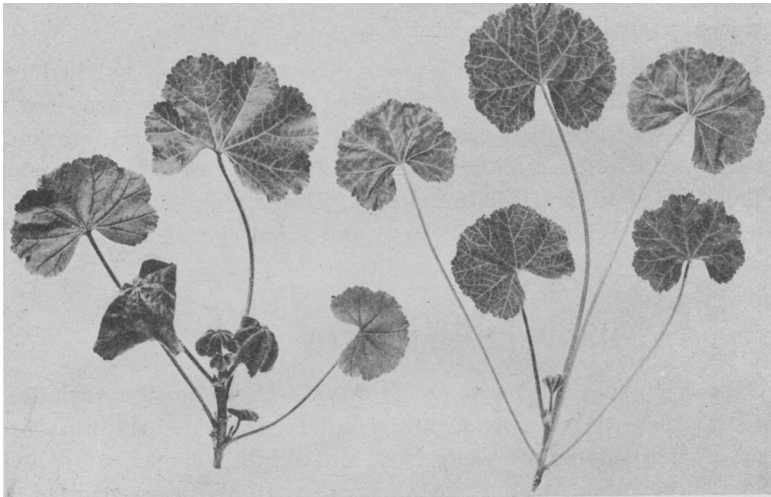


Fig. 24. Dwarf mallow (*Malva rotundifolia*): left, plant experimentally infected with curly top, showing drooping youngest leaves; right, check or control plant on which non-infective male beet leafhoppers fed.

Twenty lots of 15 non-infective males after feeding on each inoculated cotton plant were distributed on 40 beets, but not a single case of curly top developed.

The adult life on Acala cotton was as follows: males, 1-11 days; females, 4-12 days.

Weeds.—Dwarf mallow (*Malva rotundifolia*) and cheeseweed (*M. parviflora*) were proved to be naturally infected with curly top. During the 1919 and 1925 outbreaks of the beet leafhopper dwarfed mallow was demonstrated to be naturally infected with the disease in the fog belt and interior regions of the Salinas Valley. Diseased dwarfed mallow was common in the beet and bean fields and along roadsides during 1925 in the Salinas Valley. Cheeseweed showing symptoms of curly top was commonly found in the beet fields of the

San Joaquin and Sacramento valleys during 1919 and in later years. *M. rotundifolia* (fig. 24) and *M. parviflora* grown from seeds were also experimentally infected with the disease in the greenhouse.

Nymphs which hatched from eggs deposited in the leaves of *Malva rotundifolia* and *M. parviflora* under natural conditions completed their life cycle on these food plants in the greenhouse.

LINACEAE, FLAX FAMILY

Flax (Linum usitatissimum).—Flax experimentally infected with curly top was stunted, with the leaves clustered close together and twisted (pl. 4, fig. 1) at the terminal end of the shoots. The longitudinal veins were wavy with blister-like elevations (pl. 4, fig. 2). In a later stage of the disease the plant turned yellow and died. The twisting of the leaves began four days after infection.

Nymphs which hatched from eggs deposited in flax completed their life cycle.

BORAGINACEAE, BORAGE FAMILY

Borage or Bee-Plant (Borago officinalis).—Borage or bee-plant was experimentally infected with curly top in the greenhouse. The youngest leaves were curled inward with outstanding lateral veins. In the later stages of the disease, the leaves turned yellow and the plant died. Small plants infected with curly top succumbed rapidly from the effects of the disease.

The life cycle was completed by nymphs which hatched from eggs deposited in this plant.

VALERIANACEAE, VALERIAN FAMILY

Corn Salad (Valerianella locusta oleria).—Corn salad was experimentally infected with curly top. The youngest or innermost leaves of infected plants were curled and dwarfed (fig. 25). In the later stages of the disease, the plant turned yellow and died.

Nymphs which hatched from eggs deposited in corn salad completed their life history on this food plant in the greenhouse.



Fig. 25. Corn salad (*Valerianella locusta olitoria*): left, plant experimentally infected with curly top, showing curled, dwarfed youngest leaves; right, check or control plant on which non-infective beet leafhoppers fed.

ATTENUATED VIRUS

Carsner⁽¹⁾ lists the following plants under their scientific names as non-susceptible to curly top. The common names have been added.

Chenopodiaceae—

Chenopodium leptophyllum.

Chenopodium murale (nettle-leaf goosefoot).

Leguminosae—

Phaseolus vulgaris (pink bean).

Cucurbitaceae—

Cucumis melo (muskmelon).

Cucumis sativus (cucumber).

Solanceae—

Solanum nigrum (deadly nightshade).

Capsicum sp. (pepper).

Cruciferae—

Brassica oleraceae (?).

Raphanus sativus (radish).

Polygonaceae—

Rumex crispus (curly dock).

Umbelliferae—

Apium graveolens (celery).

It is evident from the results of the investigation given in this and in a previous paper⁽¹⁾ that all of the above economic plants and weeds were experimentally infected with curly top in the greenhouse and many were also proved to be naturally infected with the disease in the field. An examination of the list of cultivated plants also shows that the plants of all families with the exception of the Cucurbitaceae often required a large number of tests before a plant was experimentally infected with curly top.

In a later paper, Carsner⁽²⁾ reports that the virus of curly top becomes so attenuated when passed through certain weeds such as *Chenopodium murale*, *Rumex crispus*, and *Suaeda moquini* that it causes merely a mild form of curly top when transferred to healthy beets or other susceptible plants. The attenuated virus was transmitted from 13 of 33 plants of *C. murale* inoculated by infective beet leafhoppers, but non-infective hoppers failed to transmit the disease from 20 plants.

No experiments have been performed up to the present time to prove that the virus is attenuated in resistant cultivated plants which were naturally or experimentally infected with curly top.

SUMMARY

The following varieties of economic plants have been found to be naturally infected with curly top in California:

Solanaceae, nightshade family—

Potato (*Solanum tuberosum*): unknown variety.

Tomatoes (*Lycopersicon esculentum*): all varieties grown in California.⁽⁷⁾

Peppers: Anaheim Chili, Paprika, Pimiento, and Mexican Chili (*Capsicum frutescens*).

Cruciferae, mustard family—

Horse-radish (*Armoracia rusticana*).

Radish (*Raphanus sativas*): variety doubtful, probably Red Globe.

Cabbage (*Brassica oleracea capitata*): unknown variety.

Turnip (*Brassica rapa*): Purple Top Globe.

Umbelliferae, parsley family—

Parsley (*Petroselinum hortense*): Plain.

The following varieties of cultivated plants were experimentally infected with sugar-beet curly top:

Solanaceae, nightshade family—

Potatoes (*Solanum tuberosum*): American Wonder, British Queen, Idaho Gems, Idaho Rurals, Red Prizetaker or Improved Early Rose, White Rose, White Rose Low-Top, and Wisconsin Pride.

- Tomatoes (*Lycopersicon esculentum*): Alameda Trophy, Earliana, First Early, Globe, King of the Earlies, San Jose Canner, Santa Clara Canner, Special Early, Stone, and Wild Mexican.⁽⁷⁾
- Peppers (*Capsicum frutescens*): Anaheim Chili, California Wonder, Chinese Giant, Large Bell or Bull Nose, Long Red Cayenne, Mexican Chili, Pimiento, Red Chili, Royal King, Ruby King, Sweet Mountain, Sweet Upright, and Tobasco.
- Pepper-tomatoes: Ignacio, Novata, Petaluma, San Geronimo, Sonoma, Topepo, and Tulare.
- Tobacco (*Nicotiana tabacum*): Big Havana, Connecticut Broad Leaf, Connecticut Seed Leaf, Sumatra, Turkish, and White Burley; Peasants' tobacco (*N. rustica*).
- Cruciferae, mustard family—
- Horse-radish (*Armoracia rusticana*).
- Radish (*Raphanus sativus*): Long Black Spanish and Long White Japanese.
- Collards (*Brassica oleracea acephala*): Georgia Southern, or Creole, and True Southern.
- Garden cabbage (*Brassica oleracea capitata*): All Head Early, Early Jersey Wakefield, Early Winningstadt, Improved American Savoy, Charleston Wakefield, Large Flat Dutch, Large Late Drumhead, Mammoth Red Rock, and Surehead.
- Cauliflower, or broccoli (*Brassica oleracea botrytis*): Early Snowball, Large White Cape, Purple Cape, and St. Valentine.
- Turnip (*Brassica rapa*): Cow Horn or Long White, Early Purple Top, Flat Dutch, and Seven Top.
- Mustard (*Brassica alba*): White London mustard.
- Cress (*Barbarea vulgaris*): Fine Curled (pepper grass) and True Water.
- Polygonaceae, buckwheat or knotweed family—
- Buckwheat (*Fagopyrum esculentum*): Common Rhubarb (*Rheum raphaniticum*) Giant Crimson Winter.
- Sorrel (*Rumex scutatus*): French Large-leaved.
- Umbelliferae, parsley family—
- Coriander (*Coriandrum sativum*).
- Dill (*Anethum graveolens*).
- Florence fennel (*Foeniculum dulce*).
- Parsley (*Petroselinum hortense*): Champion Moss-Curled, Fern-Leaf Moss, and Plain.
- Celery (*Apium graveolens dulce*): Giant Pashal, Golden Self-Blanching and White Plume.⁽⁸⁾
- Salad chervil (*Anthriscus cerefolium*).
- Malvaceae, mallow family—
- Okra or gumbo (*Hibiscus esculentus*).
- Linaceae, flax family—
- Flax (*Linum usitatissimum*).
- Boraginaceae, borage family—
- Borage or bee-plant (*Borago officinalis*).
- Valerianaceae, valerian family—
- Corn salad (*Valerianella locusta olitoria*).

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PLATE 1

Pepper-Tomato

Right, leaf from Novata pepper-tomato used as a check or control on which ten non-infective male beet leafhoppers fed. The other six terminal shoots or leaves are from six varieties of pepper-tomato plants each experimentally infected with curly top by 10 infective males. Upper row, right to left: Novata, Ignacio, and Petaluma pepper-tomatoes; lower row, right to left: Tulare, San Geronimo, and Sonoma pepper-tomatoes.



PLATE 2

True Water Cress (*Barbarea vulgaris*)

Fig. 1. Terminal shoots and leaves of True Water cress experimentally infected with curly top. Terminal shoots show shortened petioles of youngest leaves. Leaves show inward roll of leaflets. The right-hand leaf in the upper row shows blister-like elevations on the lower surface of terminal leaflets.

STRAMONIUM (*Datura stramonium*)

Fig. 2. Terminal end of plant experimentally infected with curly top, showing dwarfed youngest leaves. Insert, leaf showing transparent venation.



Fig. 1

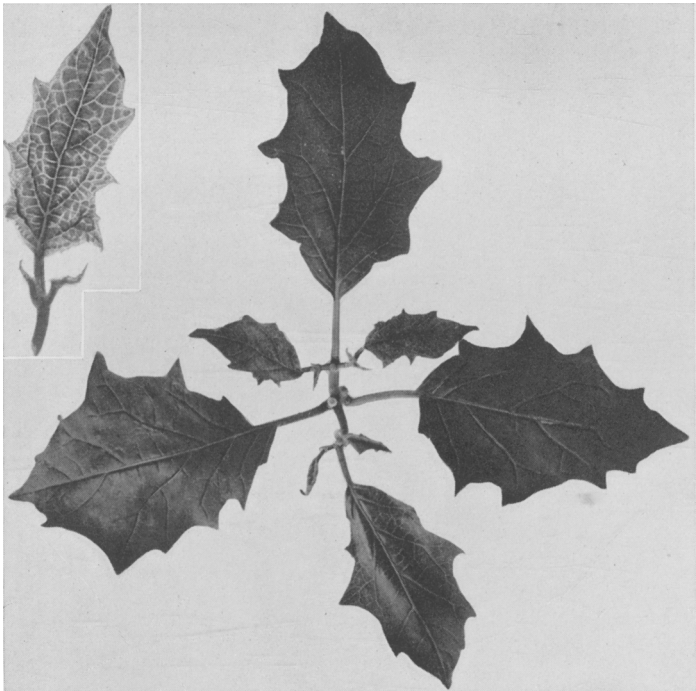


Fig. 2

PLATE 3

Horse-Radish (*Amoracia rusticana*)

Fig. 1. Horse-radish plants grown from different root cuttings. The two at the right were white when planted and are assumed to be healthy. The three in the center were white when planted, but discolored when dug, and show the spindly growth from a large number of eyes scattered at different places over the roots. The three at the right were discolored when planted and gave also very poor growth from many eyes. Courtesy M. B. McKay.

Fig. 2. Cross and longitudinal sections of horse-radish roots infected with curly top, showing dark discolorations. Courtesy M. B. McKay.

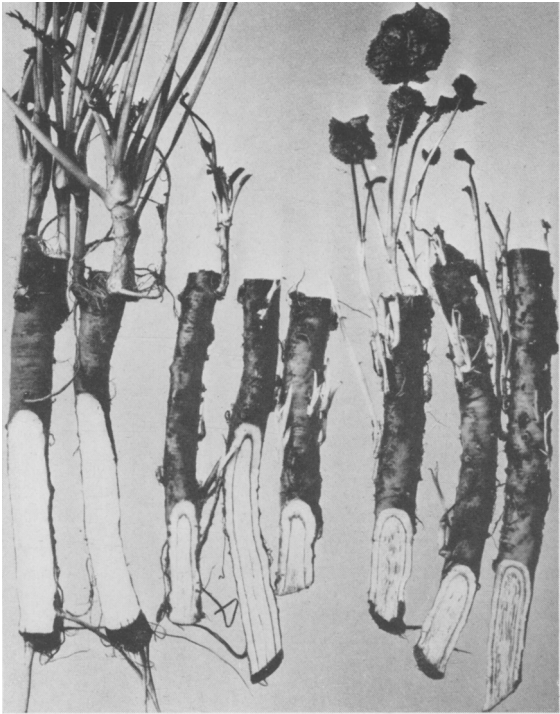


Fig. 1

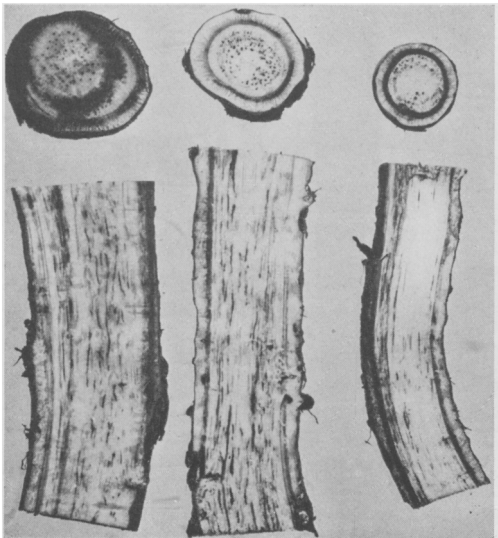


Fig. 2

PLATE 4

Flax (*Linum usitatissimum*)

Fig. 1. Left, shoot of check or control plant on which non-infective beet leafhoppers fed; right, tip of a plant experimentally infected with curly top, showing leaves clustered close together and twisted at the terminal end of the shoot.

Fig. 2. Leaves from an infected plant, showing wavy longitudinal veins with blister-like elevations.



Fig. 1



Fig. 2

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
3. The Formation of Sodium Carbonate in Soils, by Arthur B. Cummins and Walter P. Kelley. March, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. E. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. E. Hoagland. November, 1923.
13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and H. T. Bartholomew. January, 1924.
15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Velh Meyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of *Asparagus officinalis*, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.

